

From SINNESORGANE IM PFLANZENREICH

by Gottlieb Haberlandt

V. Insectivores: *Drosera* and *Drosophyllum*

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We must thank Charles Darwin (1876) for much of our knowledge about the behavior of insectivorous plants. In the case of the species of *Drosera*, his investigations established with greater accuracy than ever before, the sensitivity of the tentacles of these plants to both mechanical and chemical stimulation. Such stimuli cause the stalks of these tentacles to bend inward, and a chemical stimulus has a longer lasting effect than a mechanical one.

Nevertheless, the tentacles are extraordinarily sensitive to contact. Even a small piece of human hair, 0.203 mm long and weighing 0.000822 mg, caused the tentacle stalk to move when placed on the gland (Darwin, 1876).

Darwin further established that mechanical stimulation requires a body to contact the surface of the gland itself.¹ The body must, therefore, first penetrate the drop of mucilage covering the gland. He believed that excitation resulted from stationary pressure. Pfeffer (1884) corrected this notion by noting that, as with tendrils, frequently repeated stroking or friction with a solid body is necessary for stimulation. The individual strokes need not be strong, indeed, they may be quite weak; even the vibrations caused by rearranging furniture in the laboratory will suffice. The tentacles of *Drosera* bend more strongly the longer such stimulation continues; but stimulation lasting only three seconds had a noticeable effect in the case of very sensitive specimens.

The mechanical and chemical sensitivity of the tentacles is exclusively confined to the secretory cap (Fig. e). The

stalks are not sensitive. This is particularly worth mentioning because the small multicellular papillae which occur on the stalks might possibly be taken for perception organs for mechanical stimuli. But Darwin (1876) had already explained these papillae, which, by the way, occur

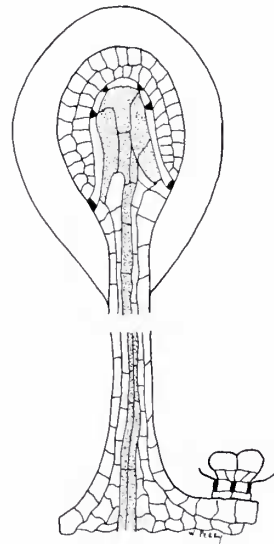
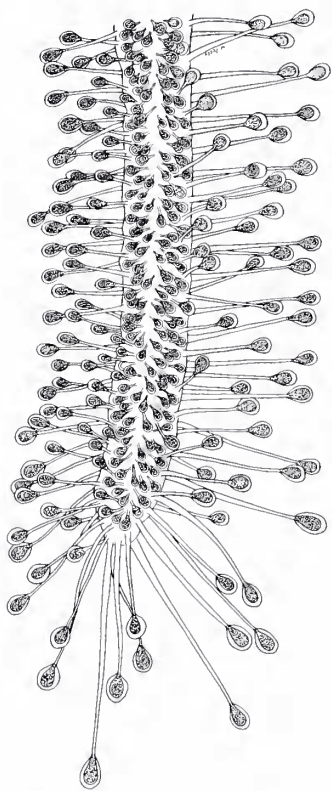


Fig. e. Longitudinal section through a tentacle and a sessile gland of *Drosera capensis* L. The secretory cap is the double layer of cells just beneath the mucilage coat over the tentacle head. Haberlandt believed these were sensory cells. His drawings of individual cells of *Drosera* tentacles are of cells in this layer. The layer between the secretory cap and the stippled cells is the endodermis and the stippled cells are the vessels of the xylem which connect with the vascular system of the leaf. There are two layers of stalk cells surrounding the xylem, an epidermis and a layer continuous with the leaf mesophyll. The drawing is by Wayne Perry.

on the entire surface of the leaf, as absorption organs, and O. Rosenberg (1899) also agrees with this view in his detailed work about the absorption processes of the *Drosera* leaf.

For this reason, we expect to find probable organs of perception for mechanical stimulation of the tentacle only on the small secretory caps, and more particularly, on their surface cell layer¹. We must, of course, remember that the small secretory caps perform very diverse functions: they secrete abundant mucilage and the digestive enzyme, they perceive mechanical and chemical stimuli, and finally, absorb the decomposed substances. All of these different functions are carried out in the glandular layer of the cap.



A 2.5 cm long tip of a *Drosera capensis* L. leaf. Figure c illustrates a longitudinal section through one of the tentacles and one of the sessile glands which would occur over the flat surface of the leaf between the tentacles. This drawing is by Wayne Perry.

It is therefore necessary to proceed carefully in the interpretation of the details of its structure.

Because of the agglomeration of the various functions, it seems wise first to examine the tentacle, or secretory cap of one of the *Droseraceae*, which is not sensitive to mechanical stimuli, and whose tentacle stalks do not move when stimulated. One such plant is *Drosophyllum lusitanicum*, a low undershrub with long, lineate, grooved leaves, with two types of glands: stalked "tentacles" and sessile, disk-shaped glands on both sides, but especially on the underside (Fig. f). Opinions differ as to the function of these glands and the division of labor existing between them. Darwin believes that the acid, very sticky secretion of the stalked glands is not secreted more abundantly after chemical stimulation. He also believes that the secretion has only a slight digestive ability. On the other hand, the glands absorb their own secretion very quickly when they are mixed with a small quantity of a nitrogenous substance². Neither after chemical nor after mechanical stimulation do the tentacle stalks move in the slightest. The sessile glands only begin to secrete when they are chemically stimulated, but it is mainly this secretion which has digestive properties and causes a rapid decomposition of the insect bodies. Goebel (1891) essentially agrees with Darwin's conception. But while he considers the stalked mucilage-secreting glands to be mainly for the purpose of trapping prey, he attributes the secretion of the digestive enzyme primarily, if not exclusively, to the small sessile glands.

Arthur Meyer and A. Dewevre (1894) have arrived at another conception. They consider the stalked glands to be the actual digestive glands, but admit also that the sessile glands have an influence on the digestion. "The probable reason that the small glands cause the protein to go into solution more quickly is because they are responsible for removal of decomposition products." These

authors then interpret the sessile glands simply as organs of absorption. In my opinion, the reasons for which they assert this are not convincing. It is mainly the following experiment which convinced them that the sessile glands do not secrete enzymes. The mucilage of the stalked glands was very carefully removed from a certain region of the leaf, so that no mucilage from the large glands came in contact with the sessile glands. When egg albumin and small pieces of meat were placed on the small glands and observed, secretion did not take place. The meat and egg albumin dried up and finally fell off. If we were to conclude from this, that: "subsequently the small glands normally produce no digestive secretion," then such a conclusion is inadmissible, because the experiment created abnormal conditions which deviated substantially from those found in nature. Under natural conditions, the bodies to be digested reach the sessile glands enveloped in mucilage, and for various reasons, this mucilage may be a necessary prerequisite for the function of the glands. This is probable if only because the mucilage prevents the released digestive secretion from drying up. On the other hand, A. Meyer and Dewevre (1894) have not identified an enzyme in the mucilage of the stalked glands. Comparative physiology also leads me to share the view of Darwin (1876) and Goebel (1891). The sessile glands of *Dionaea* are morphologically equivalent to those of *Drosophyllum*, and these are certainly digestive glands³.

Experiments concerning the functions of the stalked and sessile glands were performed after the appearance of the first edition of Fenner's (1904) book. However, he gave such an incomplete report of the results that one can not be certain just what his experiments prove. One the whole, Fenner (1904) shares the view of Darwin (1876) and Goebel (1891) that the stalked glands function primarily as traps, and the sessile glands as organs of digestion and absorption. He believes that the stalked

glands influence the sessile glands positively, and stimulate their activity (1) by the secretion which they release, and (2) by the transmission of a chemical stimulus for which Fenner posits a system of special "conductor cells." Whether this is correct, the future must decide⁴.

I shall now proceed to describe the histological structure of the stalked glands of the *Drosophyllum*. As Darwin (1876) noted, they are shaped like little mushrooms, and consist of a stalk and a slightly convex glandular disk. This consists of two cell layers, which compose the actual glandular tissue, under which follows the "intermediate layer"⁵ (as Goebel [1891] used the term), which is supplied with cuticularized longitudinal walls. The stalk broadened at its upper end, is traversed by a vascular bundle that ends with an outspread group of thickened tracheids in a net-like pattern directly under the intermediate layer.

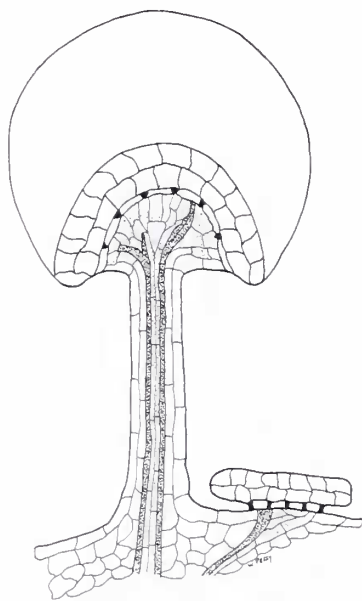


Fig. f. Longitudinal section through a stalked and sessile gland of *Drosophyllum lusitanicum*. The secretory cap is the double layer of cells just beneath the mucilage coat. Note the similarity of the cell layers with those of the *Drosera* tentacle in Fig. e. The vascular tissue has both xylem and phloem instead of having only xylem as in *Drosera*. The drawing is by Wayne Perry.

What interests us primarily is the structure of the epidermal glandular layer. As A. Meyer and Dewevre (1894) noted, this layer is covered by a relatively strong cuticle, in which however, these authors, "despite all efforts could not detect pores with certainty. When these glandular cells are killed, the red coloring material of the cell contents is quickly released and tinges the mucilage. This led A. Meyer and Dewevre (1899) to conclude that the cuticle is completely permeable, as the copious secretion of mucilage would suggest in any case. However, the porosity of the cuticle has not been established with certainty on glands with intact, or fixed protoplasts. The porosity can be very nicely observed⁶ if one examines glands whose protoplasmic cell content was completely dissolved by treatment over several hours with Javelle water⁷. If one observes the surface with sufficiently strong magnification using an oil immersion objective one can see with great clarity and extremely fine and even performance of the entire cuticle covering the glandular tissue. On sections of the gland, one observes a fine crosswise striation of the cuticle (Plate VI, Fig. 12), so that there can be no doubt about the presence of very fine, extremely numerous pores in the cuticle (this was subsequently verified by Fenner, 1904, p. 415).

The epidermal glandular cells have approximately the same height and width. Viewing the surface, one sees rather thick wall ridges projecting into the cell lumen from the slightly thickened radial walls. These ridges widen out to merge smoothly with the outer walls (Fig. 13). At deeper focus the ridges become increasingly narrow, and soon disappear completely. On longitudinal sections through the gland, one sees that the wall ridges indeed disappear toward the bottom (Fig. 12); only a few extend down to the inner wall. The cell lumen then exhibits a number of shallow recesses on its upper edge corresponding to the number of ridges. The outer walls above these recesses are no thinner than usual.

The subepidermal glandular cell layer also has these ridges; however, there are many fewer of them.

The sessile glands exhibit the same structure as the stalked glands. The epidermal glandular cell layer likewise exhibits wall ridges on the radial walls (Fig. 14); these walls, as well as the ridges, are somewhat thicker than are those of the stalked glands. After treatment with Javelle water⁷, the rather strong cuticle appears even more finely perforated than it does in the case of the large glands; I would hardly venture to interpret these extremely fine, evenly distributed perforations as an indication of the porosity of the cuticle, if the comparison with the undoubtedly porous cuticle of the stalked glands did not argue in favor of it.

If we now relate the structural characteristics we have described to the various functions of both glandular forms, it is clear, first of all, that the porosity of the cuticle facilitates and accelerates both secretion and absorption. It is also reasonable that the cuticle of the large mucilage-secreting glands is more clearly porous than that of the small glands. The even distribution of the fine pores over the entire surface of the exterior walls further argues that secretion and absorption are not localized on particular parts (e.g. those parts bordered by the wall ridges) of the outer walls.

What is the function of the ridges of the radial walls? A mechanical function, similar to that present in delicate petals, is hardly likely since the majority of the ridges do not extend down to the inner walls. It is more probable that the formation of ridges was intended to enlarge the surface area of the plasma membrane, a development which would assist in the absorption of dissolved materials and in the perception of chemical stimuli.

Drosera rotundifolia. The tentacles of this plant, so often described, have, as Goebel (1891) previously emphasized, essentially the same structure as those of *Drosophyllum*. The club-shaped end of the vascular strand which traverses the stalk is surrounded by the cuticularized "inter-

mediate layer"⁵, and this in turn, by the glandular tissue, which is mostly double-layered. The outer layer of the glandular tissue of the secretory cap has long, palisade-shaped cells on the top, which gradually become shorter on the sides. In the case of the peripheral tentacles, of course, the oblong secretory cap is shifted to the upper side of the broadened end of the stalk (Fig. e).

Contrary to the statements of Goebel (1891) and Gardiner (1885), Lily Huie (1897) has already established the existence of a cuticle on the secretory cap. I can only confirm her findings; upon treatment with sulfuric acid, the cellulose walls of the glandular tissue are quickly destroyed, and the cuticle stands out like a blister against the swollen cap. This cuticle is relatively well-developed, although it is not as thick as that of *Drosophyllum*. Both of these share the same high degree of permeability. The permeability of the cuticle is easily demonstrated by cutting off a tentacle and its stalk from a leaf that has been fixed in alcohol, and placing it in zinc chloride-iodine solution⁸. The cuticle quickly turns yellowish-brown. Immediately thereafter, the bluing of the cellulose walls of the glandular tissue also begins, and the dark blue cap stands out strikingly from the yellow-brown stalk, whose cellulose walls remain colorless because of the impermeability of their cuticle. The bluing proceeds slowly only from the cut end, just as it also disperses gradually downward from the cap to the stalk. The papillae located on the stem turn grayish-blue, indicating that their cuticle is likewise permeable. I have observed no difference in the time required for the coloration of the elongated apical glandular cells, and the lower, lateral glandular cells; therefore, all parts of the cap seem to be equally permeable.

Lily Huie (1897) tried in vain to observe the tiny pores on the cuticle of the secretory cap with a microscope. I have not been successful in this either, despite the use of apochromatic objectives. Nevertheless, I do not doubt, in view

of the directly observable porosity of the cuticle in the case of *Drosophyllum*, that the cuticle of the secretory cap of the *Drosera* is also penetrated by very fine pores⁹.

If the cap of a parietal tentacle is clarified with Javelle water⁷, one can immediately observe, with sufficiently strong magnification, a noteworthy structural peculiarity of the epidermal glandular cells. To my knowledge, this feature has remained either unnoticed, or was only vaguely mentioned, and has therefore been partly misunderstood. Viewing the surface, one immediately recognizes the same ridges present in *Drosophyllum*. These ridges extend outward from the radial walls. Here of course, they are more delicate, smaller, and also do not extend downward nearly so far as in the *Drosophyllum*; however, they do occur in greater numbers (12-15 in one cell) (Plate VI, Fig. 18). The small recesses they form are elongated to short pit canals, which project in a somewhat more slanting direction into the outer walls of the glandular cells. These pit canals are filled with little papilla-like appendages of protoplast. One can easily make these visible by soaking them for a short period in dilute sulfuric acid, and then crushing the secretory cap by pressing on the cover glass. Now the individual protoplasts of the glandular tissue emerge from the swollen cell walls fixed, and can easily be observed in different positions (Plate VI, Fig. 15 a, b, and 16). If, in addition, these are stained with toluidine blue one obtains, after successive rinsings, very beautiful and instructive slides. One can now see that protoplasts of the lateral epidermal glandular cells are supplied with a ring of tiny plasmatic papillae on the corners of their outer sides, which have a thickness of 1.5-2 μm and are approximately of equal height¹⁰. The protoplasts of the apical palisade-shaped glandular cells exhibit fewer papillae, ordinarily only on the corners of the cells. Thus in the side view, an isolated protoplast shows only two papillae on the upper corners (Fig. 17).

The surface glandular cells of the peripheral tentacles have the same structure. The cells situated on the edge of the glandular body correspond to the lateral cells of the secretory cap located on the surface, and have ridges, or plasma appendages similar to these. The centrally located cells, on the other hand, usually exhibit points, or plasma appendages only in the corners of the outer walls.

In the case of *Drosera longifolia*, the peripheral points, or plasma appendages which protrude from them are still more clearly differentiated than in *Drosera rotundifolia*. Here they are often twice, or even three times as high as wide (Plate VI, Fig. 19). The protoplasts of the apical glandular cells, which are isolated by treatment with dilute sulfuric acid and stained with toluidine blue, sometimes have a peculiar appearance: on the squat, conical upper part of the protoplast sits a cluster of 3-5 thin plasma appendages (Fig. 20). The apparent explanation for this seems to be that as the lateral walls slope inward and reduce the outer cell wall, they draw the appendages on the corners into a cluster in the center of the cell.

The apical glandular cells of *Drosera dichotoma* are somewhat different. The wall ridges are more numerous here, penetrating further toward the middle of the outer walls, and often merging with one another so that in places, they create a net whose interstices are usually elongated, and are filled with correspondingly shaped plasma appendages (Plate VI, Fig. 22). One might also mention the wide pits which occur in the outer walls. Just as in the case of *Drosera rotundifolia*, the lateral glandular cells of the cap usually only have pits on the edges of the outer walls (Fig. 21).

The structural relationships of the glandular cells of the *Drosera tentacles*, here described in detail, had already been observed by Goebel (1891) and Gardiner (1886), but they only mentioned them in passing. Goebel (1891) limited himself to the remark that the outer cell walls are pitted. In the case of *Drosera*

dichotoma, Gardiner (1886) calls these "remarkably pitted." Illustrations were not given by either of the researchers. On the other hand, Lily Huie (1897) discussed these structural relationships in greater detail, but oddly enough, she misunderstood them completely. On microtome sections she had indeed seen the wall ridges, which extend from the radial walls of the lateral glandular cells into the outer walls, and she illustrates these correctly. However, she considered them to be "toothlike" projections of the outer walls, and concluded that wide and deep pits were present but in this she was deceived. Had Huie not simply limited herself to the observation of 5 μ m thick microtome sections, but also used preparation methods which would have enabled her to visualize the subject in three dimensions, she would have noticed that the upper edge of each protoplast bears a ring of plasmatic papillae projecting into hollow cavities which are probably none other than pit chambers.¹¹

What is the function of these curious plasma appendages in the outer walls of the glandular cells? In the case of *Drosera dichotoma*, Gardiner (1886) considers the pits in which they are found to be the points from which mucilage is secreted subsequent to stimulation: but since in the case of *Drosophyllum*, the cuticle is covered with fine pores over its whole surface, and not just over the recesses, and since the cuticle of *Drosera* is very likely permeable to the same degree everywhere, I do not believe that the existence of pits in the outer walls is related to the mucilage secretion. For the same reasons, they probably also have nothing to do with the intake of substances, as Goebel presumes. Otherwise, one would also expect to find them on the outer walls of the digestive glands and absorption hairs of other insectivores. Since this is not the case, it is a well-justified assumption that the presence of pits and plasma appendages in the outer walls of the secretory cap of the *Drosera* species is connected with the high degree of sensitivity of these glands to

chemical and mechanical stimulation. And it is particularly the latter type of sensitivity which seems to offer the best explanation for their existence. Further evidence for this is offered by the case of *Drosophyllum*, whose tentacles do not respond to mechanical stimulation. Here, the recesses between the wall ridges are not elongated to form pit chambers, and plasma appendages are not present¹². I therefore consider the plasmatic papillae of the glandular cells of *Drosera* to be primarily organs of perception for mechanical stimulation. By this I do not mean to say that they do not possibly also serve for perception of chemical stimuli, and so represent tiny gustatory organs, as it were. After all, in the case of various lower animals, the same sensory organs seem to function for both touch and taste.

This conviction was strengthened by Pfeffer's (1884) investigations, which showed that tendrils exhibit the same type of mechanical sensitivity as the *Drosera* caps. Sometimes tactile pits with sensitive plasma appendages occur (Cucurbitaceae). They are, of course, distributed differently. In contrast, the plasmatic papillae of the apical glandular cells or *Drosera* are very similar to the plasma appendages of the sensory cells of the barberry anther. And this includes the manner in which they occur—namely, in the corners of the cell.

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ENDNOTES

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1. Darwin (1875, *Insectivorous Plants*) demonstrated that tentacles with their glands removed do not respond to stimulation when mechanical stimuli are applied directly to the stalk and that hard objects thrust into the mucilage will not cause movement unless they touch the head of the tentacle (see fig. e). However tentacles would also have the uppermost cells of the stalk removed or damaged. It is these cells in the uppermost part of the stalk which are deformed most when the gland is pushed with a probe and it is these cells which are homologous with the sensory cells of *Dionaea*. Elsewhere I have proposed that they are the sensory cells (Williams, 1976, Am. Philos. Soc. 120, 187-204). Firm evidence favoring a sensory role for the gland cells or for the stalk cells is lacking and the question must be left for future experiments to resolve.
2. Many of Darwin's "nitrogenous substances" such as meat, and egg-white would have contained sodium salts which Darwin himself demonstrated to be highly stimulatory to *Drosera* tentacles. The results of ex-

- periments with such poorly defined stimuli must be considered ambiguous. Meat stimulates tentacle movement but it is unclear whether it is because of nitrogenous substances it contains or because it contains sodium salts.
3. See also Fenner (1904) and Williams (1976, Amer. Philos. Soc. 120, 187-204) for a comparison of the glands of these plants. Recent work in Juniper's laboratory has greatly expanded our understanding of both the digestive glands of *Dionaea* (Robins and Juniper, 1980, New Phytol. 86, 279-327) and the sessile glands of *Drosophyllum* (Joel and Juniper, see Williams, C.P.N. 10, 36).
 4. Quintanilha (1927, Biol. Soc. Brot. 4:44-129) has done further work on this subject which is published in Portuguese with a French resume. Lloyd reviews some of this paper in *Carnivorous Plants*. Quintanilha found that stimulation of the stalked glands with albumin will result in secretion by the sessile glands and he proposes that a signal must pass from the stalked glands to the sessile glands by a pathway that is still not clear. He reports that direct mechanical stimulation of sessile glands will stimulate secretion but that mechanical stimulation of stalked glands, except in the extreme case of their removal, will not result in secretion of the sessile glands. Franca (1922, 1925) also did important work on this topic which was reviewed by Lloyd.
 5. This is an endodermis common in many plant secretory structures (c.f. Lüttge and Higinbotham, 1979, *Transport in Plants* pp. 90-92, Springer-Verlag).
 6. Schnepf (1965, Ber. dtsch. bot. Ges. 78, 478-483) has published electron micrographs illustrating pores which are 0.2 to 0.3 μm across. These pores which are somewhat larger than those of *Drosera* are near the limit of resolution of the light microscope. Haberlandt did well to observe them.
 7. Javelle water is a solution of chlorinated potash. When freshly prepared, it contains about 2.5% active chlorine. *The Merck Index*, 8th Ed., Rahway, New Jersey (1968).
 8. Zinc chloride iodine solution was a test for various polysaccharides which could be identified by the color they develop when treated with this solution.
 9. *Drosera* has been demonstrated to have pores which are just below the limit of resolution of the light microscope. Ragetli et al. 1972, Can. J. Bot. 50, 159-168; Chafe and Wardrop, 1973, *Planta* 109, 39-48; Williams and Pickard 1974, *Planta* 116, 1-16).
 10. These "papillae" are the cytoplasm that fills the spaces between the cell wall ridges. Haberlandt describes. When hardened with a fixative and isolated from their walls they have the appearance illustrated (figs. 16, 17, 19, 20). This observation does not by any means prove they are sensory receptors.
 11. The function of these ridges in the cell wall is unclear but it seems unlikely that they have a role in anything more than giving strength to the gland or increasing the membrane surface area.
 12. The lack of "pit chambers" in *Drosophyllum* is neither a necessary nor a sufficient condition for their acting as sensory structures in *Drosera*.

Nepenthes (Continued from page 64.)

regular fertilizing has only just begun. Brought into cultivation to England in the early 1900s and subsequently lost, this, the most dangerous looking *Nepenthes*, re-enters cultivation again. With luck it may be common in collections in the not-too-distant future.

I would like very much to thank Ron Zillins for the time and effort put into the excellent close-up photographs which have done this unique species justice.

(Continued on page 78.)